FURTHER OBSERVATIONS UPON THE ANATOMY OF THE INTEGUMENTARY STRUCTURES IN THE MUZZLE OF *ORNITHORHYNCHUS*.

By J. T. Wilson, M.B., Professor of Anatomy, and C. J. Martin, M.B., B.Sc., Demonstrator of Physiology, in the University of Sydney.

(Plates xlvi.-xlviii.)

In a recent paper in the Quarterly Journal of Microscopical Science,* Professor E. B. Poulton has recurred to the subject of the tactile and glandular structures in the skin of the snout of the *Ornithorhynchus*, and has given in addition an interesting account of the structure, and in part of the development, of the hairs in the same animal, with which account he has incorporated a discussion of the homologies and origin of mammalian hair in general.

It is with the earlier part of the paper, dealing with the structures in the skin of the snout, that the present writers are more particularly concerned. Mr. Poulton has done us the honour of making frequent reference to our previously published observations† upon the rod-like tactile organs (push-rods), of whose existence and general structural characters he was the first to give a description.‡

We are interested to note that part of Mr. Poulton's later work on the peculiar structures in question had been carried on contemporaneously with our own—viz., in the (English) summer of 1892. The abstract of our long-delayed paper in the Macleay Memorial Volume appeared in the published "Abstract of Proceedings of the Linnean Society of N.S.W.," August 31st, 1892,

* Vol. xxxvi. p. 143.

† Macleay Memorial Vol. Sydney, 1892, p. 190.

‡ Proc. Physiol. Soc. pp. xv. and xvi.; Journ. of Physiol. 1884.

although the title alone occurred in the "Proceedings" of the Society for that year.

In our paper in the Macleay Memorial Volume we expressed our regret at having been unable to utilise Ehrlich's methyl blue reaction upon the living tissues of the platypus snout, and ever since we have been anxious to extend our observations by means of this and also more especially by the use of Golgi's silver method. But even in Australia it is not so easy to procure living specimens of *Ornithorhynchus* and especially to have them sent on alive to Sydney, and it is only quite recently that our efforts towards again obtaining the animal alive have been rewarded with success.

Professor Poulton incidentally states his regret that we had omitted any allusion to the sweat-ducts "and their associated hair-like and nervous structures." We may state that it was the peculiarities of these structures which first of all engaged our attention and upon which in fact we wrote our first draft of a communication. On putting together our observations, however, it appeared to us that certain points remained, for the elucidation of which a further supply of fresh material was eminently desirable. Accordingly we avoided, of set purpose, all reference to the gland-ducts, and restricted ourselves to the attempt to set forth the structure of the push-rods, which appeared to be made sufficiently plain by the aid of the methods which we had up to that time been able to use.

In the introductory portion of his paper Mr. Poulton has given utterance to some rather severe strictures upon the character of the photo-micrographic illustrations which accompanied our paper in the Macleay Volume. We may at once admit the justice of much of Mr. Poulton's criticism in this regard. It is true that, as he charitably suggests, the negatives and even the proofs were very much better than the final impressions would lead one to suppose. The sections were, in point of fact, satisfactory in the highest degree; the negatives were, as we believe, very good indeed, *as photo-micrographs*, ——; while the proofs seemed at least tolerable reproductions. The ultimate results were undoubtedly the reverse of satisfactory. Nevertheless, while grateful for Mr. Poulton's

expressed sympathy, we cannot but feel that his critical instincts have led him to castigate with undue severity our well meant attempt after perfect fidelity of illustration. We feel that he has applied to photomicrographic illustrations criteria of clearness and definition only applicable to the product of the draughtsman's art. He must surely be aware that, at least in a high-power photograph of a histological subject (as distinct from the test-object of the professed photomicrographist), it is inevitable that while a few points may be rendered definite, much is necessarily out of focus and "smudgy." And even in view of his criticism we must maintain that there *are* important points brought out definitely and unmistakably in at least some of the "smudges" which inspire Mr. Poulton with horror. We would instance the lenticular bodies in fig. 10, the Pacinian-like bodies and their relations in figs. 8 and 9, the abrupt ending of the medullary sheaths of the nerve fibres in the base of the rod shown in fig. 11, the peripheral and axial groups of filaments seen in transverse section in fig. 13 (to which Mr. Poulton himself appeals further on for our discomfiture), and very specially the isolated filaments of the rod-organ shown in fig. 12. The latter figure is "smudgy" enough in all conscience, and yet the positive evidence, free from all shadow of doubt or deception, which such a photograph affords of the independence and even of structural features of the fibrils in question is perhaps sufficiently valuable to justify the exhibition of even that highly inartistic and blotchy reproduction.

Certain of the figures we are willing enough to consign to oblivion, but even did the series stand alone in all the ugliness of their imperfect reproduction, it would in our opinion be grossly unfair to pass upon them Mr. Poulton's sentence of wholesale condemnation. But it is to be noted that the photomicrographs do not, and were never meant to, stand alone, but in connection with drawings, both from nature and semidiagrammatic, which had the express purpose of elucidating and interpreting the obscurity of the photographs. With these drawings, we still believe that to the unbiassed mind the unfortunate photomicrographs may serve to convey an idea of certain of the appearances

we have described, and, so far as they go, to carry conviction of the realty of the things represented. And after all it may well enough be doubted whether a blurred uncertainty of pictorial representation is so very greatly inferior to that fatal illusory clearness of delineation so often met with, which is due to the influence of inadequate visual hypothesis upon the draughtsman. Such clearness may indeed be advantageous where no possible doubt exists as to the nature and characters of the structures to be represented, since these may in this way be made perfectly clear to the student; but on the other hand it is only too common to find erroneous hypotheses as to the nature of obscure structural details backed up by misleading drawings of the "clearest" possible description. And this observation is not made here simply as of general application. If the reader will refer to Mr. Poulton's own figures (especially his fig. 12 of Pl. XIV.) showing the structure of the "ganglion" in relation to a sweat-duct in the skin of the platypus snout, he will there see represented a collection of bodies described as "ganglion-cells," each of which is figured as duly equipped with a definite nucleus. As a matter of fact, as we shall show later on, these are not ganglion cells at all, but knob-like endings of medullated nerves,—*and they do not possess nuclei*. The appearance in a few of these bodies of a spot (to be further referred to) more or less suggestive of a nucleus, (and in some few cases, perhaps, the actual presence of a nucleus belonging to the sheath of the somewhat cell-like mass) has evidently been misinterpreted by Mr. Poulton as witnessing to the existence of nuclei in the bodies themselves. Nuclei have accordingly been clearly delineated so as to convey a quite inaccurate idea of the real nature of the "ganglion" in connection with the sweat-duct.

We are, it is needless to say, quite disposed to take for granted that Mr. Poulton's material was not of the best description, and did not afford a fair opportunity for correctly interpreting the details of these nerve structures. But what we complain of is that he has given to his drawings an utterly misleading character of clearness and definiteness by representing structural features

which we cannot but regard as almost entirely hypothetical since they are certainly absent from the (presumably) better preserved specimens in our possession.

The simplicity and clearness of semidiagrammatic delineation characterise other of Mr. Poulton's drawings than those which are by him entitled "semidiagrammatic." This is of little importance so long as the structural features are correctly given. But in his important figure 1 (really semidiagrammatic) upon which he largely relies for illustration of the general features of the push-rod, it is plain, both from his own descriptions and from his figure 4 (see also our fig. 4*), that he has omitted, in each of the three rods shown, *an entire layer of cells* (second layer of imbricated cells). If, in our attempt by photomicrography to avoid as far as possible errors such as these—arising no doubt from a laudable desire for clearness and definiteness,—we have incurred the reproach of making public, obscure and comparatively uninstructive photomicrographic illustrations, we may at least plead that these latter could not easily convey any erroneous structural hypotheses.

We shall now proceed to state the results of our continued investigations into the structure both of the push-rods and of the sweat-ducts.

I. The Push-rods.

With the fresh material recently secured we have in part devoted ourselves to the obtaining of satisfactory silver impregnations of the nervous elements of the skin of the muzzle by the use of the rapid Golgi method and to obtaining the methyl-blue reaction with the same structures by a modification of Ehrlich's method. With both methods of procedure we have achieved a fair measure of success. In order also to compare with our former highly successful gold preparations by Freud's method with bichromate tissue, we have followed Ranvier's formic-gold method for fresh tissue and have again procured very good results.

The further investigations we have thus been enabled to make into the anatomy of the push-rods in view of Poulton's late

* Macleay Mem. Vol. *loc. cit.*

criticism of some of our former statements may entitle us again to be heard in reply.

We have further completed our study of the sweat-glands and ducts and their associated structures, and we propose by means of it to supplement Professor Poulton's account of these interesting objects.

Upon the whole, as Mr. Poulton points out, our views upon the structure of the push-rods coincide with his own. The only really important subject of dispute concerns the essential nature of the fibrils or filaments which traverse the shaft of the push-rod. Poulton strongly opposes our view that these filaments are nervous in character. He appears to have interpreted our remark that he "failed to recognise the nervous character and connections of the filaments" as reproaching him with imperfect observation. It was certainly not so intended but merely as a statement of a fact, and as such, indeed, Mr. Poulton with some emphasis expresses his entire agreement with it.

We are very well aware that our opportunities for satisfactory investigation of the tissues of Ornithorhynchus are, in the nature of the case, vastly superior to those usually possessed by investigators in Europe. In view of this very fact, however, is not Mr. Poulton's dogmatic assertion that the "nervous character" of the filaments "does not exist" just a little hasty? In regard to the question of their nervous *connection* we unfortunately did not gather from Mr. Poulton's brief communication that he had "inferred" an actual continuity between nerve-fibres and the filaments in question such as we claimed to demonstrate. In the note itself there does not appear the slightest suggestion of such an inference. The title, "On the tactile terminal organs," &c., to which he appeals as sole evidence of his inference can hardly be taken as giving explicit information upon this particular point. It used to be held for example that auditory nerve fibres ended by continuity with auditory hair-cells. It has been shown pretty conclusively by Retzius, van Gehuchten and others* that these

* *Cf.* Retzius in Biolog. Untersuchungen, Neue Folge, iii. & iv.; Verhandl. d. Anat. Gesellsch. 1892, p. 63; Anatomischer Anzeiger, vi. p. 82; Van Gehuchten in La Cellule, viii. 1892.

cells are not actually connected by continuity with nerve fibres, and yet we fancy that no one would deny to the hair-cells the name of "terminal organs" of the auditory sense-apparatus.

If, however, it be admitted, as seems to be the case, that the filaments of the push-rod are, as we have described and figured them, structurally continuous, without break or interruption, with the axis-cylinders which terminate in them, then it is difficult for us to follow Mr. Poulton in his emphatic objection to regarding the former as nervous in character. He says they must be looked upon as "a new and interesting form of nerve terminal organ probably epithelial in character," but where, we ask, is there the slightest evidence for their (non-nervous) epithelial character apart from their situation in the epidermis? and of course this alone is no proof whatever that they are non-nervous. They are utterly unlike any other epithelial structure of which we are aware, and their nervous continuity is really very strong evidence against their being modified epithelial cells, for all recent investigations by Kölliker, Ramon y Cajal, v. Lenhossék and others* have shown that nowhere do sensory axis-cylinders end by actual continuity with non-nervous epithelial structures, but on the contrary by fine fibrillar often varicose end branchings in close proximity to, and contact with, epithelial cells which may or may not be specially modified. Later on we hope to give convincing proof that the fibrils under dispute are neither more nor less than just such intra-epidermic end-branchings of axis-cylinders.

Careful perusal of Mr. Poulton's statements in this connection will show that his single argument in support of his very positive opinion against the nervous character of the fibrils is the appearance they present in sections, as clear and somewhat highly refracting elements. He quotes Professor Schäfer as an authority for the view that this appearance is opposed to the theory that they are terminal nerve-fibrils. To support this argument from appearance Mr. Poulton has recourse to two

* *Cf.* Kölliker, in Verhandl. d. Anat. Gesellsch.; Ramon y Cajal, trans. in Arch. f. Anat. u. Physiol.

of our own photomicrographs. "If," he says, "they establish nothing else, they certainly prove that this conclusion as to the nature of the filaments [that they are nervous in character] is erroneous; neither naked axis-cylinders nor nerve fibrils could have caused the appearances seen in transverse section in Pl. xxv. fig. 13, and in longitudinal section in fig. 8." And why not? Apparently merely because we have clear and unstained dots and lines in two (bi-chromate) preparations stained respectively with anilin blue-black and haematoxylin, reagents which in tissues hardened with chromic salts are not to be depended upon as axis-cylinder stains. What, we must ask, are the histological criteria of nerve-fibrils and axis-cylinders? The absolute test of the nervous character is of course the histogenetic one. If these filaments are, morphologically, outgrowths or prolongations of axis-cylinders (which in turn are simply the processes of nerve-cells), then we presume that no slight histological modification of the ultimate ramifications of such a process would prevent us from assigning to them a distinctly nervous character. This we premise because we believe that these terminations of axis-cylinders (as we confidently regard them) have undergone some very slight histological or chemical modification. But it is of the utmost importance to note that whatever change may have occurred has been far too slight to affect those fundamental micro-chemical reactions to certain stains which, in the absence of the histogenetic test, constitute our ultimate criterion of their nervous character.

It was upon the strength of the argument derived from the reaction to gold salts that in our former paper we confidently pronounced these filaments to be nervous, nor should we now see any valid reason for rejecting that conclusion even if no further facts were before us.

It seems appropriate here to notice a curious little mistake Professor Poulton appears to make in reference to the gold reaction upon the fibrils. After admitting the conclusiveness of our gold-stained preparations as to the continuity of the fibrils with the axis-cylinders at the base of the rods, he goes on to say:

"It is noteworthy too that although the filaments are represented in Pl. XXVI. fig. 22 as black varicose threads, the authors accurately state in the description (p. 200) that 'the fibrils are not black but only highly refractory.'" Can it have escaped Mr. Poulton that this figure and description are those of a haematoxylin specimen and not of a gold-stained one? (Our fig. 12 gives the actual photomicrograph itself.)

In our gold preparations to which Mr. Poulton had just been referring before making this quotation, the fibrils are, of course, stained black,—or at least the darkest violet,—and stand out in most striking contrast to everything except the nerve-fibres with which they are directly continuous, as shown in our figs. 19 and 21, for whose perfect accuracy we can vouch.

It is, however, with some gratification that we are now able to present a camera lucida drawing of a push-rod (fig. 1) from a specimen impregnated by Golgi's silver method, which in the fullest and most convincing manner corroborates our former observations. Little in the way of further description seems requisite as the figure speaks for itself in a quite unmistakable fashion. From the leash of nerve fibres at the base of the rod, stained axis-cylinders are seen to ascend and to enter the base or basal part of the shaft of the rod, and then to be continued along the shaft as members both of the more peripheral circlet and of the axial group of fibres in the core of the organ. Such perfect examples as that represented were indeed far from common. We did not find that the tissue reacted at all freely towards this highly selective but rather capricious stain. All the more welcome were the few more favourable patches in which the impregnation had turned out successfully. But everywhere, almost, one could get at least partial reductions of silver showing varying lengths of axis-cylinders and terminal fibrils blackened in a precise and selective manner.

No one, we imagine, viewing the present figure, and not absolutely mistrustful of the *bona fides* of the observers and the draughtsman, can now refuse his consent to our previously

expressed dictum as to the "nervous character" of the fibrils traversing the shaft of the push-rod.

One or two minor details suggested by the figure deserve notice. The fibrils are shown as non-varicose. The apparent varicosity of the fibrils especially in our gold-stained preparations turns out to be due partly to minute sinuosities in the course of the fibrils* and partly to the presence of intercellular cement substance between the cells of the successive rows through which the filaments pass towards the surface, and which has caused reduction of the gold salts. One or two minor details suggested by the same figure seem to deserve remark.

The fibrils do not in it, nor in other of our Golgi specimens appear to be varicose as we formerly represented them in our semidiagrammatic illustrations and as they actually do appear in the haematoxylin preparation of the isolated fibrils already referred to as the subject of one of our photomicrographs† and as they also appear very distinctly in our gold-stained preparations. We have little doubt that the Golgi preparations indicate the true features of the filaments themselves and prove them to be quite smooth and sinuous, and that the varicosity as shown in specimens prepared by other methods is due to the adhesion of extraneous particles probably of intercellular cement. The regularity of the arrangement of these particles upon the filaments is doubtless due to their corresponding to the intervals between the successive rows of cells traversed by the fibrils in their course towards the surface. This view is borne out by the fact that in some parts of gold-stained preparations where the reduction was cruder and less precise than in others, the parallel series of filaments were occasionally seen to be joined by a series of dark, transverse lines, corresponding doubtless to the intervals between the successive cell elements of the core, uniting the apparently varicose points of adjacent fibrils and so giving rise to

* These sinuosities can indeed occasionally be recognised as such when haematoxylin preparations are carefully examined.

† Macleay Mem. Vol. *loc. cit.* fig. 12.

a somewhat ladder-like appearance of lines whose blurred outlines testified to the indefinite and less highly selective character of the reduction in such patches. This appearance is never to be seen in silver-impregnated nor indeed in any other kind of specimen, but it assists us in interpreting the seeming varicosity of the nerve-fibrils.

We have satisfied ourselves by careful re-examination of our haematoxylin preparation of the isolated fibrils that the beaded contour indicated in the photomicrograph is not merely an out-of-focus representation of the minutely sinuous outline seen in the Golgi, and we may add also in good haematoxylin sections (vertical) of the push-rods, and we are therefore convinced that we have given above the correct interpretation of the somewhat moniliform contour of the fibrils exhibited in some kinds of preparations.

Another point to which we may here refer is the absence from the preparation represented in fig. 1 of any evidence of branching of the axis-cylinders in the base of the rod. But that such branchings do occur our gold-preparations testify, so that there are a greater number of fibrils in the rod than there are nerve-fibres entering it. As we formerly stated the subdivision of the axis-cylinder occurs in the basal part of the rod just at the point where the medullated sheath is lost.

The figure further illustrates the connection of axis-cylinders with the Pacinian-like corpuscles, and shows in addition that other bundles of fibres extend up into the dermal papillæ. After giving off some fibres to the rod as shown in the figure these terminate in the papillæ giving off end branches, of which some at least enter the neighbouring epidermis.

We were unsuccessful in demonstrating the "nervous character and connections" of the lenticular bodies formerly described by us as lying in the base of the push-rod.

Gold-preparations, however, give indubitable testimony in support of our former statements in regard to them, and the examination of fresh preparations impregnated with methyl blue by Apathy's

modification of Ehrlich's process* has fully confirmed our conclusions. Striking views of the intermediate disc or plate between the two clear vesicular cells of the body were obtained, its nervous character being indicated by its colour reaction with the methyl blue. It bore a distinct resemblance, though on a smaller scale, to the nervè disc stained with methyl blue figured by Dogiel† in the Grandry's corpuscles, with which structures we formerly compared the lenticular bodies.

The methyl blue reaction was also exhibited by the other nervous structures in connection with the rods, viz., the nerve-fibres, the cores of the Pacinian-like corpuscles and also by the fibrils in the rod itself. Thus we have the most ample histological confirmation of the nervous character of these structures. We therefore believe that we are entitled to state definitely that these interesting filaments, in spite of their fairly definite and regular arrangement, are nothing but the end branchings of axis-cylinders of sensory nerve fibres, which have acquired a slightly specialised character from their definite relation to certain specially differentiated epidermal cells arranged so as to constitute the rod-organ.

Possibly such an example of differentiated and correlated nervous and epithelial structures may be regarded as standing midway between the ordinary intra-epidermic end-branchings of cutaneous nerves and such specialised epithelial and nervous arrangements as are found for example in the tastebuds, where also we have axis-cylinders ending freely by terminal filaments in intimate relation with far more highly specialised epithelial cells.

II.—The Sweat-ducts and their Associated Structures.

The general characters and position of these glands were described by Poulton in 1884‡ and again in the present year.§

---

* Zeitsch. f. wiss. Mikr. ix. 1, 1892, p. 15.

† Arch. f. Anat. u. Physiol. 1891, p. 182.

‡ Journ. of Physiology, Vol. v. pp. 15-16.

§ Quart. Journ. of Micros Science. June, 1894.

In his recent paper Poulton has entered more fully into their histological structure, but from the unsatisfactory nature of the material at his disposal, there remain some points which he was unable to elucidate, and others which we are convinced he has erroneously interpreted

As stated by Poulton, the gland consists of :—

(1) A terminal coiled secretory portion, which is wider than the rest of the tube.

(2) A coiled duct leading from this to the base of an epithelial downgrowth of the general epidermis.

(3) An intra-epidermal portion, pursuing a winding and irregular course through the core of the epithelial downgrowth, to open on the surface.

Poulton describes the secretory portion of the tubule as being "lined with short columnar cells surrounded by a longitudinal layer of smooth muscle-cells," and in his fig. 8, Plate XIV., outlines these latter with great distinctness. We do not think that the words "short columnar cells" well express the appearances seen by us in a large number of specimens from different animals. The cells lining this part of the duct are rather large and granular, with nuclei which stain well with ordinary nuclear stains, but the protoplasm very slightly or not at all. These cells surround a wide lumen and rest upon a basement membrane, between which and the secretory epithelium small triangular strongly staining cells are intercalated at intervals. The whole is surrounded by a sheath of fibrous tissue, but nowhere have we been able to find any trace of fusiform or muscle cells (fig. 3).

The character and arrangement of the epithelial cells in this secretory end of the duct somewhat suggest the appearance of a transverse section of the alveoli of a mucous salivary gland in mammals.

The duct leading from the secretory portion of the tube to the epidermal downgrowth consists of two layers of cells. An outer circle of short columnar cells, which exhibit a faint striation,

and whose nuclei and protoplasm stain well with haematoxylin and carmine, surrounds a cuticular layer with flattened nuclei, as described by Poulton. The whole is surrounded by a fibrous-tissue sheath (fig. 4). The duct is frequently accompanied by a leash of medullated nerves whose destination is the base of the epidermic downgrowth, which the duct enters.

The appearance and minute structure of the epidermal downgrowth with the duct traversing it are shown in fig. 2, which represents a vertical section of the organ. As to the general structure and probable significance of this downgrowth, we are in entire agreement with Poulton, who considers that it represents a modified hair follicle, through which the duct of the gland courses to the surface. The further structural particulars which we have been able to make out, tend only to strengthen Poulton's ingenious hypothesis.

The upper part of this epidermic cylinder is mostly composed of plate-like epithelial cells placed vertically to the surface. Poulton describes them as fusiform, but as they appear fusiform both in longitudinal and transverse sections of the organ, (*vide* our figs. 2, 5 and 6, or Poulton's figs. 8, 9, 10 in Quart. Journ. Micros. Science) they must in reality be flattened plates. These layers of flattened imbricated cells are arranged around the duct as a centre, but are separated from its lumen by a nucleated cuticular layer, the cells of which are irregular but generally flattened in the same direction as the plates (figs. 2, 5, 6, *c*). The individual outlines of the cells of this layer are difficult to make out, and indeed in some cases (fig. 2, *c*) the cells appear fused.

Outside the preceding layers of cells which form the core of the epithelial cylinder, but not separated from them by any sharp line of demarcation, are the investing layers of cells formed by a downgrowth from the general epidermis, the layers of which turn sharply downwards to form the peripheral part of the cylinder. These investing layers in the upper part of the cylinder consist merely of epithelial plates continuous with the more superficial parts of the general epidermis, (fig. 2, *b*) while below this there is superadded a peripheral layer of more or less cubical cells formed by

the reflection of the Malpighian layer of the epidermis. It will be observed, on reference to fig. 2, that the flattened epithelial squames of which the upper part of the core of the cylinder (probable hair shaft) is composed project vertically at the surface, and, the constituent cells becoming more or less separated from each other, form a brush-like arrangement which usually projects slightly above the general surface of the epidermis. According to our observations upon perfectly prepared material (Flemming's fluid, alcohol, and Müller's fluid), this mass of cells never constitutes a solid plug, as Poulton has figured it, but exhibits the loose and brush-like arrangement represented in fig. 2, the duct passing through it to reach the surface.

Towards the base of the cylinder, where it enlarges to form a bulb, the arrangement of cells does indeed, as Poulton points out, very strikingly suggest the bulb of a hair. This resemblance is perhaps best seen in transverse sections (fig. 6). In this situation the squames and cuticular cells surrounding the duct, which in the upper portion of the cylinder form its core, both become continuous with a mass of polyhedral cells (figs. 2 and 5, *p*). Amongst these polyhedral cells the duct of the gland passes in an irregular manner (fig. 2, *d*). The cells lining the lumen are not differentiated from the others, and their edges are ragged both here and upwards throughout the course of the duct.

Previous to entering the bulbous base of the cylinder the duct is composed of two regular layers of cubical cells (fig. 2, *d*,). At the point of entry the external layer becomes continuous with the outermost layer of cells forming the follicle, and the internal although differentiated from the polyhedral cells for a short distance, by taking the stain a little more deeply, soon becomes absolutely continuous with them.

In describing this epithelial cylinder Mr. Poulton says:—"The general epidermis is continued over it as a sheath, which strongly suggests the outer root-sheath of a hair, and between it and the cylinder itself a line of separation tends to appear." He also figures such a separation of the core from its sheath in his fig. 8. We have also noticed the same tendency of the core to shrink

away from its investing layers of cells in this position in some few specimens, but the follicle figured by us does not illustrate this. Poulton then continues—"Below, this sheath forms the outer part of the bulb, and is separated from the inner part by a space containing small branched cells, the nature of which could not be determined in my material." These branched cells are figured by Poulton in his fig. 8 *sp*. We have never seen in any of our specimens an appearance approaching that described by Poulton; the sheath of the follicle formed from the general epidermis being, as we have above described, always in contact with the polyhedral cells (figs. 2 and 6, *p*).

We now come to a part of Poulton's paper with which our observations are entirely at variance, but it is only just to state that Mr. Poulton is himself of opinion that his material was not adequate and that "the whole structure of these hair-like epidermic cylinders, and the nervous tissues evidently associated with them, is so remarkable and complex that the fresh tissues are required for their satisfactory elucidation and for the discovery of the nerve terminations which we must believe to exist in connection with the apparatus."

Poulton is quite right in describing the bulb as being invariably associated with numerous medullated nerve fibres, but we have never seen any appearances that would justify one in considering the terminations of these fibres as ganglion cells as he does. They do indeed terminate in bulbous expansions of the axis-cylinders, but not in ganglion cells. No doubt, too, Poulton's specimens did not enable him to see that large numbers of these expansions of the axis-cylinder are situated within the outer sheath of the cylinder and amongst the epithelial cells forming the outermost layer of the root sheath (figs. 2, 5, 7).

Accompanying the duct on its course to the base of the epithelial cylinder more or less closely a large bundle of medullated fibres can be seen. As they approach the base of the cylinder some of the fibres, whilst still in the dermis close to the bulb, terminate in enlarged extremities which are similar to those we are about to describe. Others pass on to the cylinder itself and

penetrate the outer fibrous sheath, entering amongst the epithelial cells forming the follicle, where their axis-cylinders suddenly expand into vesicle-like swellings, as seen in specimens stained with logwood and carmine (figs. 2, 5). The swelling of the axis-cylinder, as seen in such specimens, is faintly granular and exhibits a knotted appearance. This is seen in specimens stained by Kultschitzki's method* to be surrounded by a thin expansion of the medullated sheath, outside which again is a sharply defined nucleated capsule, continuous with the primitive sheath of the nerve fibre (figs. 2, 5, *n*).

Fresh tissue impregnated with gold chloride by Ranvier's method, or bichromate-hardened tissue stained by Freud's gold method give ample demonstration of the connections of these swellings with the axis-cylinders of the nerves (fig. 7).

We thought it possible that Golgi's silver impregnation method might show the existence of further ramifications, such as we had found to occur among the epithelial cells of the rod organs, but though by this method the end-swellings stained and their connection with the axis-cylinders was well shown, no trace of any further prolongation was to be seen. This negative result seems fairly conclusive, as the intra-epithelial ramifications of axis-cylinder branches were well impregnated in neighbouring push-rods. By no method of staining is there shown the slightest indication of nucleus in the end-swellings, although the nucleus of the capsule surrounding it, when viewed from the surface, might in some instances be mistaken for one.

Poulton's figs. 8 and 12 showing these bodies as definite nucleated ganglion cells are, therefore, quite erroneous and misleading.†

In addition to the nerve-terminations described above, Golgi preparations show leashes of fibres running upwards towards the

† Occasionally the optical transverse section of the axis cylinder before it swells out into the enlarged knob, gives rise to an appearance somewhat simulating a nucleus.

* Anat. Anzeiger, 1889, p. 223, and Zeitschr. f. wiss. Mikros. vi. 2, 1889, p. 196.

surface in the intervals between the follicle and the neighbouring epidermis. These fibres lose their medullated sheaths and terminate in branchings of naked axis-cylinders, which together with similar branchings from other sides of the follicle form a ring-like plexus around the neck of the follicle, most of the individual fibres of which have a vertical direction.

We were unable to satisfy ourselves that the terminations of these fibres entered the epidermis of the follicle. The appearance closely resembles that described by Burckhardt* and Bonnet† as occurring around the neck of the hair follicles of sensitive hairs in some mammals, and by the latter author also in the base of the epidermal downgrowths in the snout of the pig.

The further structural details we have been able to ascertain, together with the whole arrangement and termination of the nerves to the follicle, support in the strongest manner Poulton's suggestion, that the epidermal downgrowth through which the duct of the gland passes, represents a modified hair. Moreover we are of opinion that it not only structurally represents some form of modified hair, but that it is so far functionally a sensitive hair. The core of the follicle (fig. 2, *a*) does not end flush with the surface of the skin, but projects appreciably beyond. In the specimen from which fig. 2 was drawn is a fair example of this. From the relation of the cells of the core to the surrounding epithelium, one would imagine that as the epithelial cells of the follicle proliferate, the core must be pushed upwards so as to project from the surface, just as occurs with a perfectly formed hair. In this case, however, the projecting end of the core must constantly be worn away, or more probably disintegrated, leaving the appearance shown in fig. 2. Why the excretory duct of the gland should possess such a peculiar relation to it, we are at a loss to understand. The fact that, as far as we can judge, about one half of the fibres of the enormous fifth nerve in this region are associated with these supposed hairs, speaks strongly for their

* Burckhardt, "Ueber die Nervendigung in den Tasthaaren der Säugethiere."

† Bonnet, *loc. cit.*

possessing present functional importance, and indicates that they are no mere vestiges of some ancestral whiskers.

The above described mode of termination of the fibres at the base of the follicle is not peculiar. Dietl* recorded and figured somewhat similar endings in the root sheath of the sensitive hairs of the ox, cat, and dog. He described the nerve fibres as penetrating the hyaline layer of the dermic sheath and ending amongst the epithelial cells of the outermost two layers of the outer root sheath in knobbed ("knopfförmig") swellings. Dietl was uncertain whether they were indeed terminal. Bonnet† confirmed Dietl's observations and extended them to the sensitive hairs of a variety of domestic animals. He described the nerves as ending in the deeper layers of the epithelium of the outer root sheath in pale, knobbed, finely granular expansions of the axis-cylinder. These are situated in a very distinct capsule formed by the primitive sheath. Bonnet considered these expansions of the axis-cylinder as identical with the "Tastzellen" described by Merkel‡ as occurring in the same situation, but, as we think justly, denies their cellular character.

If anyone will compare figs. 14 and 15 of Plate XIX., and fig. 12 of Plate XVIII., in Bonnet's paper, with those accompanying this paper, he will find it impossible to doubt that the structures are identical in character. The first of these three figures of Bonnet represents a vertical section of the root sheath of a sensitive hair from the horse stained with osmic acid, the second a similar preparation from the snout of the pig. The third is also from the snout of the pig, and represents the base of an epithelial downgrowth stained by Löwits' gold chloride process, and might indeed well enough represent a patch of one of our gold chloride preparations of the nerve endings in the bulb of the sweat-duct.

---

* Untersuchungen über Tasthaare II. Sitzungsberichte der k. Akad. d. Wiss. Wien. Mat. Naturwiss. Klasse lxvi. Bd., iii. Abtheil. 1872.

† "Studien über die Innervation der Haarbälge der Hausthiere." Morph. Jahrbuch von Gegenbaur, Bd. iv. 1878.

In a recent paper‡ upon the anatomy of young specimens of *Echidna*, Professor W. Newton Parker describes shortly the developing sweat-glands in the skin of the snout of that animal, and, pointing out their resemblance to those described by Poulton in *Ornithorhynchus*, he expresses his dissent from the hypothesis advanced by the latter writer to explain their peculiar structure. Neither his description nor his figures appear to us to afford sufficient ground for rejecting a theory which, although without doubt antecedently improbable, is yet borne out by so many striking correspondences in structure indicated by Prof. Poulton and in the present paper.

The developmental stages studied by Prof. Parker were probably much too late to afford conclusive evidence as to the real manner of development of these structures. So, at least, an inspection of his special figure of the sweat-gland and duct on Plate II. would indicate. The only specific reference we note to an earlier condition, is the statement that "the lumen is not developed in the young stages."

EXPLANATION OF PLATES.

Fig. 1.—Vertical section of rod-organ, showing nervous arrangements, from a preparation impregnated with silver by Golgi's rapid method (× 320 diams.). At the base of the rod the axis-cylinders of the nerve fibres show out strongly. These fibres have two destinations (*a*) to the base of the rod where some join the small Pacinian bodies and the remainder penetrate the rod-organ to be continued up almost to the surface as the axial and peripheral groups of axis-cylinders. (*b*) To the sides of the rod-organ, where some enter the organ to take part in the formation of the peripheral circular group of axis-cylinder processes, whilst others pass up to the sides and tip of the papilla, where they enter the epidermis. The axis-cylinder processes apparently end in the superficial portion of the rod-organ, and are not demonstrated

‡ P.Z.S. 1894, Part i. pp. 3-14, Plates I.-III.

right up to the surface, but from the gradual way in which they are, by this method, shown to taper off at their extremities, it is probable that they participate in the corneous change which obtains in the epithelial cells of this region of the rod-organ, and do not therefore react in the same manner to the reagents as in the deeper region. The preparation was drawn with a Zeiss' camera lucida.

Fig. 2.—(× 320 diameters). Vertical section of sweat-duct traversing an epithelial cylinder (modified hair). The preparation from which this figure was taken was cut from a portion of the muzzle which showed remarkably little pigmentation. Accordingly the outlines of the epithelial cells were not obliterated by the perinuclear deposits of pigment and showed out with distinctness. It was fixed in absolute alcohol and stained with haematoxylin.

a, epithelial plates forming the core of the cylinder; *b*, epithelial sheath continuous with the superficial layers of the epidermis; b^1, epith. sheath continuous with the malpighian layer of the epidermis; *c*, cuticle of duct formed of fused epithelial cells; *d*, intra-epidermal portion of duct; d^1, infra-epidermal portion of duct; *e*, medullated nerves ending by enlargements of the axis-cylinder (*k*,) surrounded by a nucleated expansion of the primitive sheath *n*; *n'*, nuclei of nerve sheath; *p*, polyhedral epithelial cells in the bulbous portion of the cylinder continuous with *a* above.

Fig. 3.—(× 320 diameters). Section of the deepest (secretory) portion of the tube stained with haematoxylin.

a, secretory epithelium cells; *b*, small deeply stained cells wedged in between the secretory cells.

Fig. 4.—(× 320 diameters). Transverse section of excretory duct stained with haematoxylin.

a, outer layer of columnar striated cells; *b*, inner layer of flattened cells, the outlines of which are not seen.

Fig. 5.—(× 480 diameters). Transverse section through the bulbous portion of the epidermal cylinder stained with haematoxylin.

d, duct of sweat-gland; *c*, cuticular cells lining duct; *p*, polyhedral cells of bulb; *b*, plate-like epithelial cells continuous with the superficial layers of the epidermis (*vide* fig. 2); b^1, epithelial sheath continuous with the malpighian layer of the epidermis (*vide* fig. 2); *k*, terminal enlargements of

the axis-cylinders of medullated nerves supplied to this region; *n*, nuclei in expansion of the primitive sheath forming a capsule for *k*. Drawn with camera lucida.

Fig. 6.—(× 480 diameters). Transverse section of the neck of an epidermal cylinder similar to but smaller than the one from which fig. 5 was taken. Stained with haematoxylin. This section was taken in a region where the follicle was completely surrounded by dermis, *f*.

d, duct of sweat-gland, which is wider in this region; *c*, cuticular layer of cells surrounding duct; *a*, epithelial plates (*cf.* fig. 2, *a*); b^1, epithelial cells containing perinuclear pigment continuous with b^2 at the summit of the dermal papilla; b^2, malpighian layer of epidermis containing perinuclear pigment; *e*, epidermis.

Fig. 7.—(× 320 diameters). Vertical section through bulbous base of epithelial cylinder traversed by sweat duct; showing knob-like endings of medullated nerve fibres both within and without the bulb. Stained by Freud's gold-chloride method.